



Fire intensity effects on seed germination of native and invasive Eastern deciduous forest understory plants

Sarah M. Emery^{a,*}, Joy Uwimbabazi^a, S. Luke Flory^b

^a Biology Department, 139 Life Sciences Building, University of Louisville, Louisville, KY 40292, USA

^b Department of Biology, 1001 East 3rd Street, Indiana University, Bloomington, IN 47405, USA

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ABSTRACT

Low-intensity fires were important for maintaining the structure of Eastern deciduous forests (EDFs) for thousands of years before European settlement of North America, though fire suppression became a standard management practice in the 1930s. More recently, prescribed fires have been reintroduced to EDF habitats to aid in the restoration of native plant diversity, but invasions of non-native species such as *Microstegium vimineum* (Japanese stiltgrass) may increase prescribed fire intensity and suppress colonization of native species. As fire becomes a more common management tool in these habitats, it is vital to predict fire temperature effects on the native and non-native species present in the system. In this study, we found that prescribed fires in areas invaded by *Microstegium* can be 250–300 °C hotter than fires in nearby native-dominated areas. We then compared the effects of fire on germination rates of six native and three non-native EDF understory species representing the range of functional groups common in this habitat. We manipulated both fire intensity (temperature and length of exposure) and type of fire effect (direct flame and indirect furnace heat) to generate germination curves and make predictions about potential prescribed fire effects on populations of these species. There were very different responses among species to both direct (flame) and indirect (furnace) heating. Germination of three native species, *Lycopus americana* (American water horehound), *Verbesina alternifolia* (wingstem), and *Vernonia gigantea* (tall ironweed), showed signs of being stimulated by heating at low temperatures, while germination of all non-native species (*M. vimineum*, *Elaeagnus umbellata*, and *Schedonorus phoenix*) were inhibited at these lower intensities. High fire intensity (temperatures above 300 °C) effectively killed most species, though one native species, *Senna hebecarpa* (American senna) and one non-native species, *E. umbellata* (autumn olive), were capable of tolerating 500 °C temperatures. We conclude that high-intensity prescribed fires in habitats invaded by *Microstegium* may reduce seed germination of some non-native species, but may also inhibit the regeneration of native understory species.

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1. Introduction

1.1. Fire history in Eastern deciduous forests

Low-intensity fires were important for maintaining the structure of Eastern deciduous forests (EDFs) for thousands of years before European settlement of North America (Brose et al., 2001; McEwan et al., 2007; Boerner et al., 2008). Native Americans used low-intensity spring and fall surface fires to manage EDF habitats for increased fruit and berry production, to prepare sites for agriculture, to control pest species, to maintain open woodlands for wildlife, and to concentrate game species (Delcourt and Delcourt, 1997; Brose et al., 2001; Ruffner and Groninger, 2006). Fire frequency in woodlands during this period was decadal (Brose et al., 2001). Oaks (*Quercus* spp.) were particularly adapted to this fire regime, and regeneration of oaks was correlated with frequent fires (Abrams, 2005). Tree ring analyses have indicated that following European settlement of EDF areas in the early 1800s, fires occurred as often as every 6–7 years as pioneers maintained Native American burning practices (Brose et al., 2001; McEwan et al., 2007). However, most understory species which are native to EDFs do not often show adaptations to fire, such as serotiny (fire-dependent seed dispersal), which may indicate that a natural fire regime (e.g., lightning strikes) involved only infrequent fires (Glasgow and Matlack, 2007a).

After 1880, high-intensity fires became more common in this region due to industrialization of logging practices (Brose et al., 2001). After a period of relatively frequent fires, fire suppression became a standard management practice in the 1930s (Brose et al., 2001; Ruffner and Groninger, 2006; McEwan et al., 2007). This practice

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* Corresponding author. Tel.: +1 502 852 5940; fax: +1 502 852 0725.

E-mail address: sarah.emery@louisville.edu (S.M. Emery).

Table 1

Plant traits and germination requirements for species used in heating experiments. Information gathered from the following sources.

Species	Native/non-native status	Family	Functional group	Known germination requirements: cold treatment	Known germination requirements: peak germination temperatures	Known germination requirements: Light: Dark cycle
<i>Elymus villosus</i>	Native	Poaceae	Cool season perennial grass	No cold stratification required ^a	Unknown	Unknown
<i>Lycopus americanus</i>	Native	Lamiaceae	Forb	270 days cold stratification ^b ; no cold stratification required ^{c,d,a}	Peak germination at 20–30 °C ^b	Unknown
<i>Paspalum laeve</i>	Native	Poaceae	Warm season perennial grass	No cold stratification required ^c	Unknown	Unknown
<i>Senna hebecarpa</i>	Native	Fabaceae	legume	No cold stratification required but needs scarification ^c	Unknown	Unknown
<i>Verbesina alternifolia</i>	Native	Asteraceae	Forb	Cold stratification, but length not specified ^b	Peak germination at 15–30 °C ^b	L > D ^b
<i>Vernonia gigantea</i>	Native	Asteraceae	Forb	Unknown	Unknown	Unknown
<i>Elaeagnus umbellata</i>	Non-native	Elaeagnaceae	Shrub	Cold stratification 90–112 days ^b ; Without stratification germination ranges from 40–50% ^e	Peak germination at 10–30 °C ^b	L > D ^b
<i>Microstegium vimineum</i>	Non-native	Poaceae	Warm season annual grass	Unknown	Unknown	Unknown
<i>Schedonorus phoenix</i>	Non-native	Poaceae	Cool season perennial grass	No cold stratification required ^c	Unknown	Unknown

^a Prairie Moon Nursery (Winona, MN) recommendations.^b Baskin and Baskin (2001).^c USDA NRCS Plants Database (2009).^d Heartland Restoration (Ft. Wayne IN) recommendations.^e Fowler and Fowler (1987).

tice resulted in slowed regeneration of fire-tolerant oaks, while fire-sensitive woody native species such as maples (*Acer* spp.), tulip poplar (*Liriodendron tulipifera*), and black cherry (*Prunus serotina*) have increased dominance (Abrams, 1992; Iverson and Hutchinson, 2002; Iverson et al., 2008). Additionally, fire suppression may well have facilitated invasion by fire-intolerant non-native species, similar to patterns found in western North American forests (e.g., Keeley, 2006).

1.2. Prescribed fire and invasive plants

Attempts to restore oak dominance and create open forest habitat now often involve prescribed fire (McEwan et al., 2007). Prescribed fires can be successful at increasing recruitment survival, and growth of oak seedlings by opening the forest canopy (thereby increasing light availability) and reducing litter (e.g., Green et al., 2010; Royse et al., 2010), though this is not always the case (e.g., Albrecht and McCarthy, 2006). In addition, disturbance-dependent non-native species may take advantage of recent fire disturbances to invade new habitats (Grigulis et al., 2005; Jacquemyn et al., 2005; Glasgow and Matlack, 2007b). Some invaders may also consequently increase fire intensity, with negative consequences for native plant regeneration (Mack and D'Antonio, 1998; D'Antonio, 2000). For example, invasion of Australian savannas by the African bunchgrass *Andropogon guyanus* greatly increased fuel loads and increased fire intensity 8-fold, reducing native tree cover and diversity (Rossiter et al., 2003). The complicated interaction between fire, native plant regeneration, and non-native plant invasion makes it difficult to predict the effects of reintroducing fire in EDF habitats.

Microstegium vimineum (Japanese stiltgrass) is one particular invasive species of EDF habitats that has the potential to drastically alter fire regimes. It is a native of Asia that was first documented in the U.S. in Tennessee in 1919 (Fairbrothers and Gray, 1972). It has recently spread throughout the Eastern U.S. and currently ranges from Texas to New Jersey (Barden, 1987; Morrison et al., 2007),

thriving in disturbed sites of EDF habitat (Barden, 1987; Adams and Engelhardt, 2009). *Microstegium* is known to produce abundant biomass, and litter is slow to decompose in the fall (Ehrenfeld et al., 2001). Similar to grass invasions in other habitats, this may drastically alter fire dynamics in EDF due to shifts in fuel loads (Brooks et al., 2004). Thus, *Microstegium* invasion may indirectly alter EDF biodiversity by altering fire dynamics.

One potential insight into this problem is gained by understanding the effects of fire intensity on seed germination of both native and non-native understory species. Fire often cues a “flush” of seed germination due to litter removal and newly open canopy (Witkowski and Wilson, 2001; Brys et al., 2005; Glasgow and Matlack, 2007a). However, if fires are extremely intense, then high temperatures at the soil surface may be lethal for seeds (e.g., Herrero et al., 2007; Reyes and Trabaud, 2009). Native and non-native species may have different responses to fire intensity. For example, while a few understory species native to EDF rely on low-intensity fire for germination (e.g., Hoss et al., 2008), high-intensity prescribed fires can stimulate germination of non-native understory species such as *Rosa multiflora* (Glasgow and Matlack, 2007a).

Opposing effects of fire on seed germination can become important in predicting the spread of non-native species. Many invasions are driven by seed availability as well as by disturbance (Tilman, 1997; Lockwood et al., 2005). For example, a study of three forest invaders in Pennsylvania and New Jersey found that propagule pressure and canopy disturbance were more important predictors of invasion than herbivory or habitat species diversity (Eschtruth and Battles, 2009). In another study, persistence of non-native *Microstegium* populations in forests was highly dependent on the seedbank near the soil surface (0–5 cm depth, Gibson et al., 2002). Fires can enhance seed germination by increasing canopy openness, and can decrease germination by raising soil temperatures at shallow depths and directly burning seeds caught in the litter layer. Depending on the plant species and fire intensity, fire may

slow invasions by reducing seed viability, or may actually accelerate invasions by increasing seed germination rates and opening the forest canopy.

As fire becomes a more common management tool in EDF and other habitats, it is imperative to be able to predict fire effects on the species present in the system. In this study, we compare effects of fire on germination rates of several native and non-native EDF understory species. We manipulate both fire intensity (temperature and length of exposure) and type of fire effect (direct flame to mimic direct seed burning in litter or standing dead plant material, and indirect furnace heat to mimic air and soil heating) to assess potential fire effects on seed germination in *Microstegium*-invaded and uninvaded EDF habitat. We then produce germination curves and make predictions about potential prescribed fire effects on population dynamics of these species.

2. Methods

2.1. Effects of *Microstegium* invasions on prescribed fire temperatures

To determine how *Microstegium* invasions affect prescribed fire intensity, we measured prescribed fire temperatures in invaded and nearby reference areas at Big Oaks National Wildlife Refuge in Madison, IN (38°49'33"N, 85°22'50"W). We established six 10m × 25m paired permanent plots in three separate units (~40–850 ha) scheduled to be burned in late March 2009. Invaded plots were located in areas with dense, nearly continuous stands of *Microstegium*, and reference plots were located as near as possible in similar habitats free from invasions. We housed HOBO U12 data loggers fitted with Type K thermocouples (Onset Computer Corporation, Pocasset, MA) inside waterproof containers (Pelican Products US, Hyrum, UT) and buried them ~10 cm deep at six locations in each permanent plot. Thermocouple wires were mounted to re-bar at 10 cm above the soil surface to record fire temperatures reached in flames just above the litter layer (avg. flame heights among plots 21–57 cm, Flory unpublished data). Seeds in standing dead biomass would be directly exposed to flames at this height. Loggers were set to record one measurement per second. Measurement locations were arranged in a 2 × 3 grid within each plot such that locations were separated by 3.5–6.5 m. Trees, fallen logs, and other potentially confounding objects were avoided. Prescribed fires were conducted on 18 and 23 March, 2009 by first lighting backing fires with standard drip torches on the downwind sides of the units and then lighting head fires. Fire temperature data were processed with HOBOWare Pro v. 2.6.0 (Bourne, MA).

2.2. Study species

We examined effects of fire on seed germination of 6 native and 3 non-native invasive EDF species. The native species were *Elymus villosus* (hairy wildrye), *Lycopus americana* (American water horehound), *Paspalum laeve* (field paspalum), *S. hebecarpa* (American senna), *Verbesina alternifolia* (wingstem), and *Vernonia gigantea* (tall ironweed). The non-native species were *Elaeagnus umbellata* (autumn olive), *M. vimineum* (Japanese stiltgrass), and *Schedonorus phoenix* (tall fescue; formerly known as *Festuca arundinacea* Schreb.). Hereafter species are referred to by genus only. The native species are all commonly found in lowland forest habitats or in disturbed successional areas where *Microstegium* is most invasive in this region (Gleason and Cronquist, 1991; Jones, 2005). Many of the species used in the experiment were found in abundance at Big Oaks National Wildlife Refuge. For example, we surveyed 29 sites separated by 100 m–22 km and found that *Elymus* occurred at 52% of the sites and *Senna* and *Verbesina* each occurred at 21% of sites

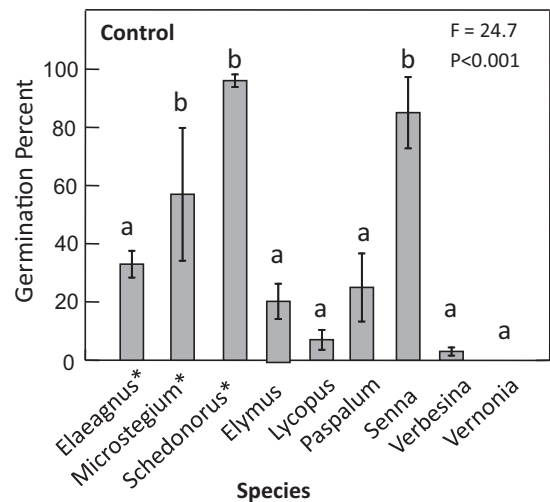


Fig. 1. Germination of three non-native (*) and six native species under control (25 °C) conditions. Different letters indicate significant differences among species as determined by Tukey pairwise comparisons. Error bars represent ± one SE.

(Flory, unpublished data). While these species represented only a small subsample of the native diversity in these habitats, we chose a variety of functional groups (warm season grasses, cool season grasses, forbs, and legumes) to attempt to generalize our results to other native species. Further, the species used were all either widely available for seed collection in the field or readily available from commercial suppliers, and required little cold stratification for germination (Table 1). In Fall 2009, *Elymus*, *Microstegium*, and *Verbesina* seeds were collected from Big Oaks National Wildlife Refuge and *Senna*, *Paspalum*, and *Schedonorus* seeds were collected from the Bayles Road research site in Bloomington, IN (39°10'27"N, 86°30'23"W); in spring 2010 *Vernonia* seeds were obtained from Prairie Moon Nursery (Winona, MN); *Lycopus* seeds were provided by Heartland Restoration Services (Ft. Wayne, IN), and *Elaeagnus* seeds were provided by Sheffield's Seeds (Locke, NY). All seeds were air dried in paper envelopes at room temperature, and stored at 4 °C until germination trials began in late spring 2010. One species, *Senna hebecarpa*, required ten days of cold/wet stratification as well as physical scarification, which was achieved by gently rubbing seeds with sandpaper.

2.3. Flame treatment

To test for direct effects of fire on seed germination (as would occur if seeds were trapped in the forest litter layer), we exposed seeds to a Bunsen burner flame (as in Sweet et al., 2008). To flame seeds, we used forceps to hold each treated seed in a Bunsen burner flame (temperature range between 300 and 400 °C) for one of four different time lengths: 3, 6, 9, or 12 s. We had five replicates consisting of 20 seeds for each species and treatment combination. To insure a constant flame temperature, we held each seed at the same height above the burner, and used a type K-thermocouple to verify flame temperatures between runs. Twenty seeds of a species were treated consecutively, then placed on moist filter paper on top of wet vermiculite in a petri dish, sealed with parafilm, and placed under fluorescent growth lights in the lab (at approximately 25 °C) on an 18:6 light:dark cycle to stimulate germination. While this does not mimic field germination conditions for these species, the germination temperature and light cycle does fall within the peak range for all species on which we could find information (Table 1). We also germinated five replicates of 20 seeds of each species that had not been exposed to fire to establish baseline (control) germination rates (Fig. 1). After 2 weeks, germinated seeds in each petri

Table 2
LD₉₀ values for three non-native (nn) and six native (nat) species under different heat treatments as calculated by a quadratic model. Values that were infinite are represented by "n/a". Missing values indicate germination at that temperature was never greater than 10%. Values indicated with an asterisk (*) are based on non-significant curve fitting. Values indicated by ** are based on a best-fit linear model.

Species	Flame LD90 (s)	100 °C LD90 (s)	200 °C LD90 (s)	300 °C LD90 (s)	400 °C LD90 (s)	500 °C LD90 (s)
<i>Microstegium</i> (nn)	3.62	60.6	23.4			
<i>Elaeagnus</i> (nn)	4.18	n/a	52.6	30.02	22.3	22.6
<i>Schedonorus</i> (nn)	3.97	2635**	23.6	20.7		
<i>Elymus</i> (nat)	1.22	122.3				
<i>Lycopus</i> (nat)		54.7**	38.6			
<i>Paspalum</i> (nat)	3.43	50.6*	22.5			
<i>Senna</i> (nat)	6.91	168.4**	57.1	29.2	25.2	9.9
<i>Verbesina</i> (nat)		83.5*	23.6			
<i>Vernonia</i> (nat)	3.04	68.2				

dish were counted, which were identified by the presence of an emerged radical or cotyledons. Dishes were re-sealed and left for another two weeks to determine if additional seeds germinated. For each dish, a germination fraction (# germinated seeds/total # seeds) was calculated.

2.4. Furnace treatment

We used a muffle furnace (Thermo Fisher Scientific, Waltham, MA) to test for indirect effects of fire on seed germination, as would occur if seeds in the soil were heated (as in Tarrega et al., 1992; Herranz et al., 1998). Twenty seeds of a given species were put into a small aluminum foil package (to keep seeds from "popping" in the furnace) and placed in the furnace at one of five temperatures: 100, 200, 300, 400, and 500 °C. For each temperature treatment, we exposed seeds to heat for five different lengths of time: 5, 10, 20, 40, and 60 s. Each temperature × time combination was replicated five times (20 seeds per replicate) for each species. After heating, seeds were germinated as described above.

2.5. Data analysis

To compare fire intensity in our prescribed fires, we calculated the number of seconds fires at each location in each treatment reached or exceeded temperatures of 100 °C, 200 °C, and 300 °C, as well as the maximum temperature at each monitoring location. We square-root transformed count data to better meet normality assumptions, and used 2-sample *t*-tests to compare differences in fire temperatures between invaded and reference sites.

For our laboratory experiments, a germination probability curve was generated for each species at each furnace temperature and flame exposure based on collected germination data. Control seed germination was treated as 0 s of exposure in order to generate curves. Three different models were compared for best fit of each curve: a linear model, a quadratic model, and a logarithmic model (data not shown). In most cases, the quadratic model provided the best fit for the germination data, though in a few cases a linear model provided the best fit. From these probability curves, the LD₉₀ (lethal-dose) value for each species–temperature combination was calculated. The LD₉₀ value is the exposure time needed to kill 90% of the seeds of a given species at a given temperature (Sweet et al., 2008). These values represent estimations of the amount of time a fire would need to be active to kill the vast majority of seeds in an area. As we did not directly assess final seed viability with dissection methods, our LD₉₀ values may overestimate actual seed mortality. However, especially at higher temperatures, often only burnt bits seeds were left after treatment, reinforcing that these seeds were dead rather than long-term dormant.

We also examined whether heating treatments had an overall inhibitory or stimulatory effect on seed germination of each species

at each temperature by calculating average germination rates of the heat treatments (averaging across all time exposure lengths until all seeds of all species were dead) and dividing this value by the average germination rates of the control treatment (no heat). We added one percent to all control germination numbers to avoid zeros in the denominators of species with no germination under control conditions. With this metric, values greater than one indicate that heat acted as a germination stimulator and values less than one indicate that heat was a germination inhibitor. We used one-way ANOVA to compare these heating effects across species. All analyses were performed in SYSTAT v.12 (SYSTAT Software Inc, 2007).

3. Results

3.1. Effects of *Microstegium* invasions on prescribed fire temperatures

Prescribed fires in *Microstegium*-invaded sites had significantly higher temperatures than nearby invader-free reference sites (Fig. 2). Maximum fire temperatures were 300–400 °C hotter in invaded sites than reference sites ($F_{1,35} = 68.42$, $p < 0.001$), and temperatures of 100, 200, and 300 °C were sustained for longer periods of time (by 20–30 s) in invaded sites (100 °C: $F_{1,35} = 5.31$, $p = 0.028$; 200 °C: $F_{1,35} = 75.11$, $p < 0.001$; 300 °C: $F_{1,35} = 157.42$, $p < 0.001$).

3.2. Flame treatment

Senna was the species most tolerant of direct flame exposure, with a predicted LD₉₀ value one and a half to two times longer than

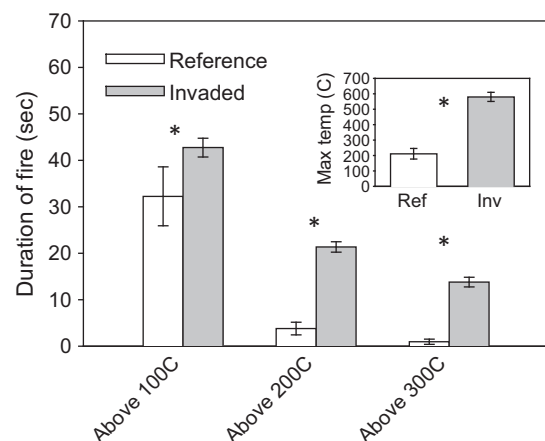


Fig. 2. Duration of prescribed fire temperatures at 100, 200, and 300 °C, and maximum temperature values (inset) in invaded and reference (uninvaded) sites. Asterisks (*) indicate significant differences at the $p = 0.05$ level. Error bars represent \pm one SE.

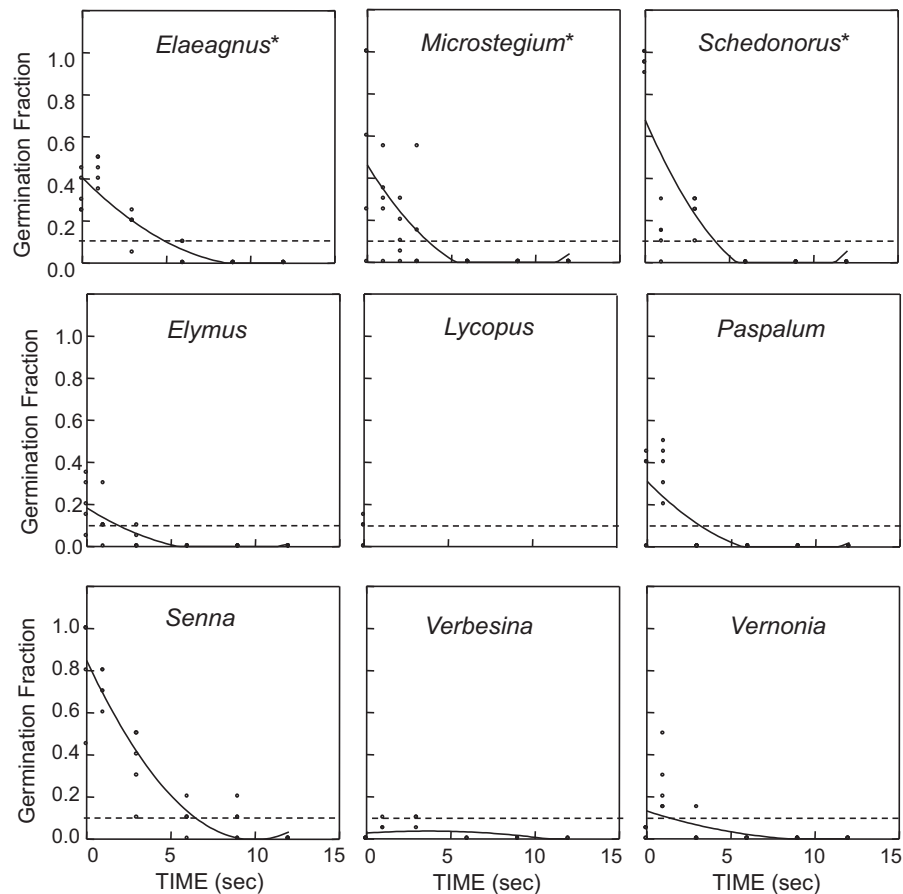


Fig. 3. Germination curves under the flame treatment for three non-native (*) and six native species. Dashed lines indicate 10% germination rates. LD₉₀ values were calculated where the germination curve reached 10% germination. Similar methods were followed to calculate LD₉₀ values for furnace treatments as well (not shown).

all other species (Table 2). The native species *Verbesina* and *Lycopus* had extremely low or no germination with the flame treatment, and so have no LD₉₀ value (at no temperature did they ever reach 10% germination) (Fig. 3). The three non-native species all had LD₉₀ values of 3–4 s. For all species, LD₉₀ values were substantially shorter for the direct flame treatment than for any of the indirect furnace heating treatments.

For the three non-native species, direct flame reduced germination by 50–90% (Fig. 4). *Schedonorus* was most strongly inhibited by fire, with germination reduced by almost 90% (though this was not significantly different from the other non-native species). Germination of the native species had more varied responses to direct flame. While *Senna* was capable of tolerating direct flame the longest, direct heat actually had an inhibitory effect on this species (Fig. 4). In fact, only two species, *Vernonia* and *Verbesina*, showed evidence for germination stimulation by fire. *Verbesina* did not germinate at all in the control treatment, but had low germination with direct flame for short periods of time (1–3 s). Similarly, *Vernonia* had very low germination rates in the control treatment (3% on average), but slightly higher rates when exposed to direct flame. One native species, *Elymus*, showed strong inhibitory effects with germination reduced by more than 50%. All other native species were only moderately inhibited (no more than 50% reduction in germination).

3.3. Furnace treatments

Most species could tolerate long exposure times to indirect heat at low temperatures (Table 2), but germination rates of a few species were actually stimulated by 100 °C warming. In particular, *Lycopus* and *Verbesina* showed 2–5-fold increases in germination

(Fig. 4). Both of these species had fairly low germination rates under control conditions (less than 10%). Only *Paspalum* and *Vernonia*, both natives, were negatively affected by heating at this low temperature, with germination rates reduced by about 50%.

Temperatures above 200 °C inhibited germination rates for all species (Fig. 4), and killed all *Elymus* and *Vernonia* seeds. For most other species, exposure to 200 °C temperatures for longer than 25 s was capable of killing 90% of seeds (Table 2). *Lycopus*, a native species, was more tolerant of 200 °C temperatures, taking close to 40 s to reach LD₉₀.

Indirect heating for any length of time above 300 °C killed all *Microstegium*, *Lycopus*, *Paspalum*, and *Verbesina* seeds. Heating above 400 °C killed all *Schedonorus* seeds. Only two species, *Senna* (native) and *Elaeagnus* (non-native), could tolerate indirect temperatures above 500 °C, with *Elaeagnus* having twice as long LD₉₀ exposure time at this temperature (Table 2, Fig. 5).

4. Discussion

Data collected from prescribed fires in our study indicated that average maximum fire temperatures in *Microstegium*-free areas were around 200 °C at 10 cm above the forest floor, while fires in *Microstegium* invaded areas had average maximum temperatures closer to 580 °C. Additionally, fires in *Microstegium* invaded areas had longer periods of temperatures above 100, 200, and 300 °C. Based on the performance of species in the lab, we predict that very few species would be capable of tolerating direct burning of thatch in fires through *Microstegium* invaded areas. However, seeds in the soil seedbanks of these sites may be protected from the more intense temperatures above. While we did not directly measure

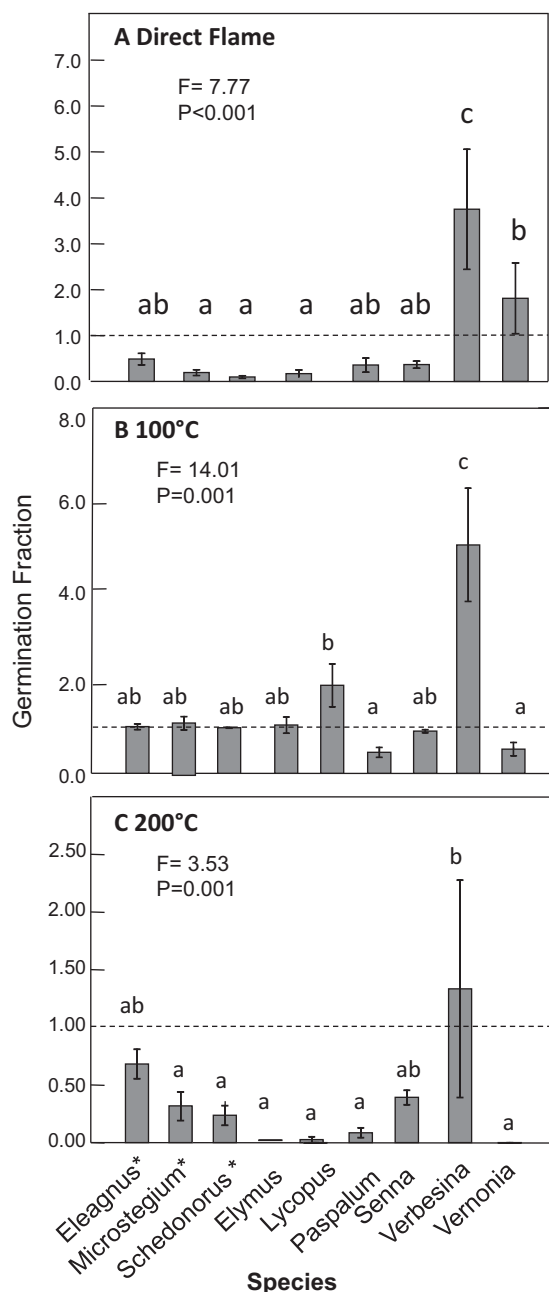


Fig. 4. Germination fraction (# seeds germinating in heat treatment/# seeds germinating in control) of seeds under direct flame (A), 100°C (B) and 200°C (C) heat treatments (note different y-axis scales). Non-native species are indicated by asterisks (*). The dashed line indicates where germination did not differ between the control and heat treatment. Values above the dashed line indicate stimulation of germination, values under the dashed line indicates inhibition of germination by heat. Different letters indicate significant differences among species as determined by Tukey pairwise comparisons. Error bars represent \pm one SE.

soil temperatures during prescribed fires in our study, it is common for temperatures at the soil surface to reach 600°C or more during burns of fire-prone systems such as chaparral, while temperatures at just 2–3 cm soil depth may be closer to 100°C (Baskin and Baskin, 2001). Soil temperatures may be even less affected in deciduous forests, because of higher moisture levels and insulating ability. For example, prescribed burns in deciduous forests of Ohio averaged 220°C at the forest floor, but soil temperatures at 1 cm depth were only raised 5–20°C during the burn (Iverson and Hutchinson, 2002). Thus, understory EDF species that are trapped

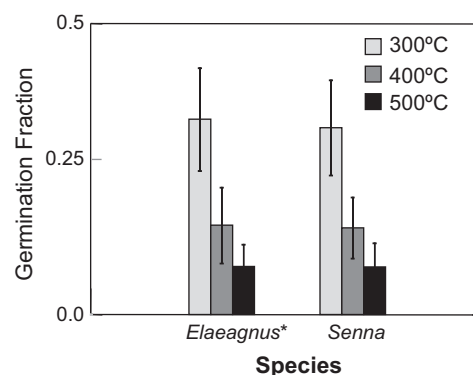


Fig. 5. Germination fraction of the two species capable of germinating under high heat treatments. The non-native species is indicated by an asterisk (*). There were no significant differences between *Elaeagnus* and *Senna* germination fractions at these higher temperatures (300°C: $F=3.39$, $p=0.07$; 400°C: $F=2.38$, $p=0.13$; 500°C: $F=0.03$, $p=0.88$). Error bars represent \pm one SE.

in the litter layer are much more likely to be inhibited by fire than those that are at or below the soil surface.

This study also demonstrates the wide range of responses to fire across plant species in EDF habitats. Some of this variability may be due to the somewhat unrealistic germination conditions in our experiment. However, to our knowledge, nothing has been published on the fire responses of the majority of species used in this study, nor on many herbaceous native EDF species in general. Given that our experiments evaluated fire effects on a variety of functional groups of both native and non-native species, we believe that at least some generalities can be taken from our results. While we are unable to statistically compare performance of native and non-native species as general groups, only native species (i.e., *Verbesina*, *Vernonia*, and *Lycopus*) showed any evidence of greater germination with low heat exposure. The native species generally had low germination rates without heat exposure (20% or less, with the exception of *Senna*), and so low-intensity fire may stimulate regeneration of these species in EDF.

While most species in this study were not able to germinate after exposure to temperatures above 200°C, two species, *Elaeagnus* and *Senna*, were quite tolerant of high temperature conditions, germinating even after exposure to 500°C temperatures. Heat may have acted as a germination stimulant for *Senna* in particular. The only legume in our study, *Senna* seeds required breaking of physical dormancy through breakdown of the tough seed coat (Baskin and Baskin, 2001). However, as we mechanically abraded the seed coat of this species before fire treatments, this mechanism is probably only partly responsible for *Senna*'s success with fire. Both *Elaeagnus* and *Senna* represented the largest-seeded species of those we tested, and so may remain viable longer due to increased protection by the seed coat (Baskin and Baskin, 2001; Pyke et al., 2010). As a caveat, seed size is not always a good indicator of heat tolerance (Hanley et al., 2003). It is important to note that *Elaeagnus* is the only woody understory species evaluated in our study, is a non-native invader of forest edges, and is also known to vigorously re-sprout after damage from fire or cutting (Yates et al., 2004). For these reasons, fire is not expected to be a useful management tool in areas invaded with this species.

The non-native grass species *Microstegium* and *Schedonorus* both had high seed germination rates (60–90%), which may in part explain why these species are so successful at invasion (Cheplick, 2005). As annual plants, *Microstegium* populations are especially dependent on seed germination and establishment every year (Gibson et al., 2002). Fires above 100°C strongly reduced germination rates for both of these species. This indicates that even low-intensity prescribed fires may be useful for controlling these

species. However, *Microstegium* in particular is known to have large seed bank stores with seeds persisting up to five years in the soil, so occasional prescribed fire may have little effect on establishment rates of this species (Gibson et al., 2002; Flory and Lewis, 2009). Similarly, even reducing germination percentages by 90% in a given year may not effectively control populations if other demographic stages are more important for overall population growth (e.g., Buckley et al., 2004; Shea et al., 2005). Additionally, established invasive grasses are generally quite tolerant of fire (D'Antonio and Vitousek, 1992; D'Antonio, 2000) and any reductions in seed germination may be offset by greater light and nutrient availability. Studies in barrens and grassland habitat invaded with *Schedonorus* have shown only very small reductions (e.g., 5%) in extant populations after prescribed fire (Madison et al., 2001; Rhoades et al., 2002), while one study in deciduous forests in Ohio showed that fire actually increased germination of *Microstegium* seeds in canopy gaps (Glasgow and Matlack, 2007a).

5. Conclusion and management implications

Based on the results in this study, we predict that prescribed fire in EDF habitats will have strong inhibitory effects on seeds in the litter layer or those still attached to standing dead plants, where seeds would be exposed to direct flame or high indirect temperatures, but only if temperatures at the soil surface reach 200 °C or more. Low intensity fires, such as are increasingly implemented through prescribed burning in EDF habitat, may actually enhance germination of native species without strongly altering non-native species. However, in habitats invaded with *Microstegium*, fire temperatures are substantially hotter, and will likely decrease germination of both native and non-native species. If a manager's main goal is to control *Microstegium*, then high-intensity fire should be effective in killing seeds found in the litter layer. However, seed banks will serve as an important germination source for regrowth of the understory after prescribed fires. Additionally, other non-native species which are tolerant of high-intensity fire, such as *Elaeagnus*, may take advantage of a decrease in *Microstegium* and native species abundance to invade. While understanding the probable responses of seeds to prescribed fire may help in the development of tools for successful management of EDF habitat, the entire life cycles of targeted species should be considered before settling on a management strategy.

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